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Nesting Biology of Two North American Species of *Chelostoma* (Hymenoptera: Megachilidae)

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Abstract.—Nests of *Chelostoma phaceliae* Michener and *C. minutum* Crawford are described for the first time. *C. phaceliae* nested in abandoned burrows that other insects bored in stems of elderberry (*Sambucus*). *C. minutum* nests were recovered from 2 mm diameter borings in trap blocks. Both species separated their cells and plugged the nest entrance with soil. Data on next architecture, provisions, cocoons, sex ratio, and nest associates are presented. Chalkbrood, a fungal disease of bees, killed 4.7% of the *C. minutum* larvae.

Bees in the genus *Chelostoma* Latreille occur in both the old and new worlds, and their zoogeographical distribution includes the Holarctic and Oriental regions (Griswold 1985). Adults are small, non-metallic, and slender. Information on nesting biology is limited. Parker and Bohart (1966) noted *C. phaceliae* Michener was reared from trap-stems, Stephen et al. (1969) gave information on cell linings and material used in nest construction by *C. minutum* Crawford, and Eickwort (1981) discussed the biology of two adventive species now established in New York. In Europe, both of these latter species utilized beetle borings and one was reared from trap-stems (Bonelli 1967). Hurd (1979) reported that native North American *Chelostoma* were oligoleges of Hydrophyllaceae because of the numerous collections made from *Phacelia* and *Eriodictyon* flowers. This study presents more detailed data on the nesting biology of *C. phaceliae* and *C. minutum,* including nest architecture, factors affecting mortality of immatures, sex ratios, and identity of pollen used to provision cells.

METHODS AND MATERIALS

Nests of *C. phaceliae* were obtained from stems removed from live plants of elderberry (*Sambucus*) that grew near the banks of the Truckee River north of Verdi, Nevada (Washoe Co.). The stems were collected during the winters of 1961–1964. Nest contents from such stems were recorded and individually placed in gelatin capsules and reared after a 2-month cold treatment at 5°C. In these earlier studies, placement of sexes within the nest and weight of the adults were not recorded.

Nests of *C. minutum* were recovered from trap blocks placed at several sites in the mountains near Logan, Utah. At each site, 10 trap blocks (Fig. 1) with 5 layers of drilled wood (each layer had 10 holes, 2 each with diameter of 2, 4, 6, 8, and 10 mm

Figure 1. Trap nest utilized in this study.

for a total of 50 holes/trap) were individually attached to wood stakes placed 50 m apart. The stakes were driven into the ground and traps were held about 1 m above the soil. The experiment began in May and the traps were removed in early October. Methods of recording data and rearing contents from traps were described earlier (Parker 1985).

Data on adult weight (separated by sex) from each site were analyzed by analysis of variance. If $P < 0.05$, Fisher's LSD multiple comparison test was used.

Chelostoma minutum

Nesting Sites.—In Logan Canyon, 10 sites were established and numbered from the entrance to the summit of the canyon. Elevation differed by about 100 m between adjacent sites. At sites 3, 4, and 8, nests of *C. minutum* were recovered; at the lower sites (1876 to 1976 m), the dominant trees were juniper, scrub maple, and box elder. At site #8 (2134 m), the dominate trees were fir, aspen, and mountain mahogany. Two other sites on the west side of Cache Valley in the Wellsville Mountains (1982 m), where the dominant trees were aspen, maple and box elder, also had numerous *Chelostoma* nests.

Nest Construction.—All nests were obtained exclusively from 2 mm wide borings. A total of 90 nests was recovered from all the sites. A total of 509 cells was produced and the average number of cells/nest was 5.65 (range of 1–14, SD = 3.6). The percentage of 2 mm borings utilized at sites where *C. minutum* nested ranged from 3 to 62.

Females of *Chelostoma* rarely used the rear section of the 100 mm deep borings. Instead, nests were begun an average of 46.2 mm (SD = 29.6 mm, n = 57) above the inner end. The partitions separating the cells and forming the base of the first cell were made from thin discs of soil which averaged 0.7 mm thick (SD = 0.2 mm, n = 172). The average length of cells (by emergent sexes) was: female = 6.2 mm

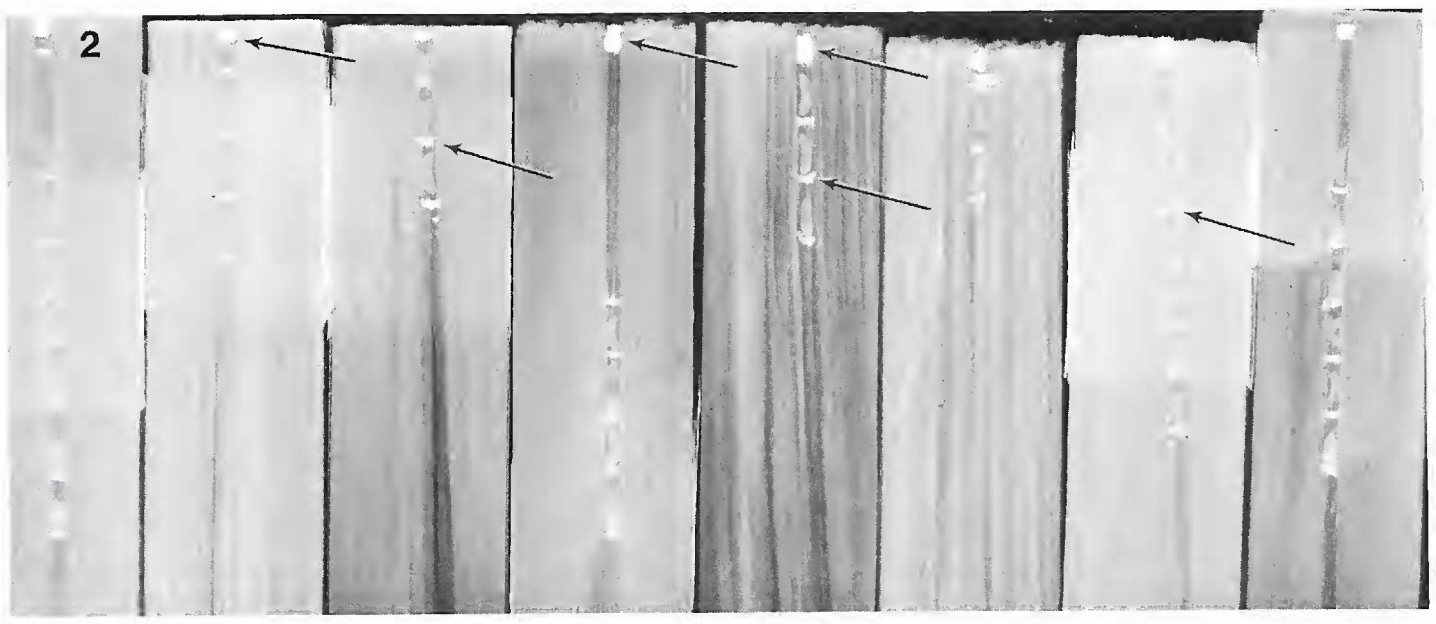

Figure 2. X-radiograph of nests of *C. minutum*. White areas (arrows) indicate nest plugs and cell partitions.

long, (SD = 1.0 mm, n = 56), male = 6.1 mm long (SD = 1.1 mm, n = 56). Often, the last cell in a nest series was longer than cells below it because the entrance plug served as the top of the cell. Average length of these long cells was 36.3 mm (SD = 21.5 mm, n = 26). A vestibular cell was made in some (13%) of the nests; average length of these cells was 15.7 mm (SD = 19.5). The entrance to the boring was usually closed (83% of the nests) with a thicker (2.6 mm, SD = 1.1 mm, n = 75) plug of soil (Fig. 2). Often, the entrance plug had several larger pieces of gravel stuck together with sand and probably a salivary secretion. Some plugs also contained small amounts of organic matter.

Provisions.—The moist pollen-nectar provisions were packed into the lower 3/4 of the cell. The top of the provision was slanted and formed a shelf on which the egg was deposited. *Allium* pollen grains made up the majority of the provisions and ranged from 97.5 to 100% of the plant species used by *C. minutum* at all but one location. At two sites in Logan Canyon, the provisions were exclusively pollen from *Allium*. At the highest elevation in Logan Canyon, no *Allium* pollen was found in the nests; only *Phacelia* and *Sedum* (?) pollens were identified.

Feces.—The shape of the fecal pellets formed by *C. minutum* larvae was variable; some were globular and others elongate. Most pellets were deposited beneath the partition at the top and along the sides of the cell (Fig. 3).

Cocoon.—The cell walls below the partition were closely lined with a thin, transluscent layer of white silk that held the fecal pellets against the side and beneath the cell partition. This first layer formed a hood over the actual barrel-shaped cocoon. Cocoons were made from a single layer of silk, were very thin, and often ripped apart when the boring was split open.

Overwintering.—The overwintering stage was a prepupal larva. A few larvae (0.8%) failed to develop further the first year, but all died during the second year and before they reached the adult stage.

Sex Ratio and Adult Weights.—Combined sex ratio from all sites was 1.05 males: 1 female. However, the sex ratio differed among sites. For example, at one site in

Figure 3. Cocoons formed by *C. phaceliae* larvae.

Logan Canyon, the sex ratio was 2.0 males: 1 female, but across the valley there were more females than males—0.88 males: 1 female. Average weight of adults differed among sites and between sexes. At site #4 in Logan Canyon, males averaged 3.06 mg and females weighed an average of 3.75 mg. These differences were significant ($P < 0.05$, male n = 44, female n = 22, ANOVA). At the Wellsville site across the valley, males also weighed less (average of 2.69 mg) than females (3.19 mg, $P < 0.05$, male n = 53, female n = 78, ANOVA). The weight of the respective sexes differed significantly between these sites ($P < 0.05$, ANOVA). Thus, individuals from nests made at higher elevations weighed less than those from nests at lower elevations. There were no significant differences in the expected sex ratio calculated from data on adult weights (see Torchio and Tepedino, 1980, for methods). The expected ratio was 1.2 males: 1 female at Logan Canyon and Wellsville, which was similar to the actual sex ratio based on combined data (see above). Placement of the sexes within the nest was typical of most bees that nest in linear series; females were in the first cells constructed and males were in cells constructed later (Table 1). In unusually long nests (13–14 cells), some females were in the outer cells. Placement of the sexes in long nests may have resulted from supersedure.

Mortality.—Death from unknown causes averaged 36.3% of the immature stages. The pine wood used to construct the nests may have been an important factor in this unusually high larval mortality. Resins from the wood surrounding the small boring seeped often into the nest and soaked into the provisions. Bee cells in such nests contained provisions with dead eggs or dead young larvae. Within-nest temperatures may have also affected larval mortality. In some nests, the provisions lost their shape and flowed the length of the cell, thus submerging eggs and/or young bee larva.

Nest Associates.—No parasites were found in any cells of *C. minutum,* but the common nest-destroying larvae of the beetle, *Trichodes ornatus* Say, consumed

Table 1. Contents of *Chelostoma minutum* cells from trap blocks placed in the vicinity of Logan, Utah 1984.

Cell Position	*Females*	*Males*	*Dead*	*Ascosphaera*	*Trichodes*	*Misc.**
a	33	5	33	7	4	8
b	25	19	30	8	3	4
c	22	33	24	4	2	3
d	10	18	18	4	2	2
e	7	18	16	1	1	3
f	10	9	19	0	1	0
g	7	14	13	0	1	0
h	6	12	8	0	0	0
i	3	8	11	0	0	0
j	3	8	5	0	0	0
k	2	7	3	0	0	0
l	0	4	2	0	0	2
m	1	2	0	0	0	0
n	1	0	0	0	0	0
Total	137	130	182	24	14	22

*Cells partially finished, missing data, or larvae injured during rearing.

2.8% of the cells. An important disease organism, the fungus *Ascosphaera* which causes chalkbrood in leafcutting bees (McManus, 1983), was found in 4.7% of the cells. Parasitism in the first cells constructed was higher than in cells constructed later (Table 1).

Chelostoma phaceliae

Nesting Site.—Nests of *C. phaceliae* were found only in borings in stems attached to living elderberry plants. The bees appropriated the burrows of other aculeates (*Ceratina* and *Ectemnius*). *C. phaceliae* did not nest in elderberry trap stems at many localities near Verdi (unpublished data from another experiment). These traps were placed vertically in the ground.

Nest Construction.—Only six nests of *C. phaceliae* were found during these studies although thousands of nests of other aculeates were recovered from borings in elderberry stems (Parker and Bohart, 1966). The number of cells/nest ranged from 2 to 10 and averaged 4.3 (SD = 3.0). Most of the nest material was lost subsequent to these studies, and complete data on nest measurements were not available. The length of cells containing males averaged 6 mm and those containing females averaged 7 mm. In one nest made in a 3 mm wide boring, the entrance plug was 4 mm thick. This nest was initiated above the bottom of the boring. The cell partitions and the entrance plug were made from small grains of sand that had been stuck together with a salivary secretion.

Feces and Cocoons.—There were no discernible differences in the shape of the fecal pellets and the construction of the cocoon between *C. phaceliae* and *C. minutum*. The irregular shaped fecal pellets of *C. phaceliae* are shown in Fig. 2.

Provisions.—The single nest sampled had 100% *Phacelia* pollen in the provisions.

Sex Ratio.—No data were recorded on sex ratio and adult weight.

Discussion

Griswold (1985), in a revision of the systematics of bees in the tribe Osmiini, suggested that *Prochelostoma* should be synonymized with *Chelostoma*. Biological data also support this suggestion since nesting characteristics, i.e. material used for nest construction, occurrence of natural nests in beetle burrows, formation of the cocoons (Krombein, 1967), are very similar in these genera. The gross morphology of *Chelostoma* prepupae (Fig. 2) is similar to those of *Hoplitis*; prepupae of both are linear rather than the curled or c-shape typical of *Heriades* and *Ashmeadiella* prepupae. Cocoons formed by larvae of both *Hoplitis* and *Chelostoma* had a hood that holds the fecal pellets against the upper cell walls and cell partition.

Hurd (1979) reported *Chelostoma* females were oligoleges of Hydrophyllaceae, but in light of this study and data referenced by Eickwort (1980) on adventive species, the range of floral resources utilized by *Chelostoma* for nest provisions is broader than was previously believed. In Europe, Kapyla (1978) reported that *C. campanularum* Kirby and *C. fulginosum* were oligoleges of *Campanula* (Campanulaceae). In New York, these inventive populations also were associated with *Campanulum* (Eickwort, 1981). The range of floral resources used by *C. minutum* appears to be made on the basis of availability rather than specialization as previously believed (Hurd, 1979), since provisions at nesting sites in Utah contained Liliaceae pollen.

Nesting sites chosen by species of *Chelostoma* appear to be specialized, both in location and in size of the boring. The great number of traps with larger borings set out each year by researchers in our laboratory, in which no *Chelostoma* were captured (unpublished data), indicates that hole size is an important factor in choice of nesting sites. Hole sizes larger than 2 mm were never used by *Chelostoma*. In Utah, it was not uncommon to locate natural nests of *C. minutum* made in old beetle exit holes in standing dead trees. Traps placed on such trees were readily accepted by *Chelostoma* (unpublished data). Trap stems, however, placed at the same sites where *Chelostoma* nested in block traps during an eight-year study (unpublished data), were not utilized by *Chelostoma*.

Stephen et al. (1969) reported that *C. minutum* lined its cells with pitch and gravel and "lines its burrow with a transparent varnish that appears to be secreted." None of the nests examined in this study contained resin and the transparent burrow linings were not apparent.

The presence of the fungus, *Ascosphaera,* in cells of *Chelostoma* is noteworthy. *Ascosphaera* spp. causes chalkbrood, a general term for such diseases of both honey bees and leafcutting bees. A modern classification of these fungi is urgently needed because many species or forms have been associated recently with solitary bees (unpublished data) and little information concerning identification or host susceptibility is available. At this point, it is difficult to determine whether these diseases are spreading from infected populations of the alfalfa leafcutting bee, which are produced in enormous numbers each summer throughout the western portion of the United States, or if the fungi associated with *Chelostoma* and other solitary bees are new species. Little research has concerned the cross-infectivity or the influence of hosts on morphological and biological characteristics used to distinguish species of *Ascosphaera*.

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